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REDUCTION OF PROVISIONING EFFORT IN RESPONSE TO EXPERIMENTAL MANIPULATION OF CHICK NUTRITIONAL STATUS IN THE HORNED PUFFIN

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Abstract. Using a supplemental feeding experiment, we investigated the ability of adult Horned Puffins to decrease provisioning effort in response to reduced nutritional requirements of chicks. We found no difference between experimental and control groups in parental provisioning before supplementary feeding was initiated. After receiving supplemental food for seven days, experimental chicks grew faster, gained more mass and received 87% less food from their parents than did control chicks. These results demonstrate that Horned Puffin parents can decrease food provisioning in response to a decrease in their chick nutritional requirements.

Key words: *Fratercula corniculata*, *Horned Puffin*, *nutritional status*, *regulation of food provisioning*, *re-productive effort*, *seabirds*.

Reducción del Esfuerzo de Aprovisionamiento en Respuesta a la Manipulación Experimental del Estatus Nutricional de Pichones en *Fratercula corniculata*

Resumen. Usando un experimento de suplementación alimenticia, investigamos la habilidad de adultos de *Fratercula corniculata* de disminuir el esfuerzo de aprovisionamiento en respuesta a una reducción en la demanda nutricional de los pichones. No encontramos diferencias entre grupos experimentales y control en el aprovisionamiento parental antes que la suplementación de alimento fuera iniciada. Luego de que los pichones recibieron comida adicional durante siete días, los pichones experimentales crecieron más rápido, ganaron más peso y recibieron 87% menos alimento de sus padres que los pichones control. Estos resultados demuestran que los padres de *F. corniculata* pueden disminuir el aprovisionamiento en respuesta a una reducción en los requerimientos nutricionales de sus pichones.

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For animals that reproduce more than once, the benefits of investment in a single reproductive event must

be balanced against costs that limit future reproduction (Stearns 1992). The allocation of limited resources between reproduction and adult survival is of particular interest in long-lived species (Erikstad et al. 1997). Since a small reduction in the adult survival of long-lived species has a large negative impact on lifetime reproductive success (Charlesworth 1980), life-history theory predicts that trade-offs in resource allocation between parents of such species and their offspring should favor the needs of the parent (Mauck and Grubb 1995). Examination of the mechanisms involved in the regulation of reproductive effort may help to identify trade-offs associated with reproduction in long-lived species.

Among avian species, seabirds are characterized by long life spans, deferred maturity, and low annual reproductive output (Charlesworth 1980), traits generally thought to reflect the high temporal and spatial variability in marine food supplies (Lack 1968). Parental food provisioning is a relatively easily manipulated component of reproductive effort in long-lived seabird species, and many studies have examined the regulation of reproductive effort and the ability of parents to modify their provisioning behavior according to chick need (e.g., Johnsen et al. 1994, Granadeiro et al. 2000).

The ability or willingness of parents to adjust provisioning in response to chick demand varies both among species and among individuals. Results from a range of seabird species have shown that some seabird parents provision independent of their chick's current requirements (Ricklefs and Schew 1994, Takahashi et al. 1999), while others have provided evidence for provisioning adjustment in response to chick need (Bolton 1995, Hamer et al. 1998, Granadeiro et al. 2000). The degree to which parents adjust provisioning in response to their offspring's demand for energy may be influenced by species-specific foraging constraints, such as the distance from the breeding colony to the feeding area (Ricklefs 1987, 1992, Weimerskirch et al. 1995, Hamer and Hill 1997), or nocturnal, single-meal provisioning habits (Takahashi et al. 1999). An individual's response to chick need may also depend on the current body condition of the adult (Johnsen et al. 1994, Erikstad et al. 1997, Tveraa et al. 1998), the size of their chick (Erikstad et al. 1997), and temporal variation in local food availability.

Comparative study of the regulation of food provisioning among lineages or tribes, and among species within the same lineage with both similar and differing feeding ecology, may clarify the different selective pressures involved in the regulation of parental provisioning. Among seabird species, the four species of puffin (tribe *Fraterculini*; Strauch 1985) are particularly suitable for investigations into the dynamics of parental provisioning because they are long-lived, produce a single-egg clutch, feed their chicks whole, fresh fish, and, with the exception of the Rhinoceros Auklet (*Cerorhinca monocerata*), make several food deliveries per day. The adjustment of provisioning effort in response to chick demand has been examined in the Atlantic Puffin (*Fratercula arctica*; Hudson 1979, Harris 1983, Johnsen et al. 1994, Cook and Hamer 1997, Erikstad et al. 1997, Wernham and Bryant 1998) and

the Rhinoceros Auklet (Welham and Bertram 1993, Bertram et al. 1996, Takahashi et al. 1999).

There is growing evidence for the ability of Atlantic Puffins to adjust provisioning in response to chick need. In an experimental study, Wernham and Bryant (1998) demonstrated that Atlantic Puffin parents can decrease rates of provisioning to chicks given supplementary food. Using a similar manipulation on a closely related species with similar diurnal foraging habits, our study tested the parental response of Horned Puffins (*Fratercula corniculata*) to the experimentally reduced nutritional requirements of chicks. According to our hypothesis that adult Horned Puffins can adjust their provisioning effort in response to the nutritional requirements of their chick, we predicted a decrease in provisioning to the supplemented chicks.

METHODS

STUDY AREA AND SPECIES

The study was carried out on Duck Island, in western Cook Inlet, Alaska (60°09'N, 152°33'W). Fieldwork was conducted between July and August 1998. Duck Island has an area of approximately 2.4 ha and maximum elevation of 49 m. The majority of the estimated 4000 Horned Puffins nest in caves in the cliffs and in crevices among boulders.

Horned Puffins lay a single egg that is incubated by both parents for an average of 39–41 days (Piatt and Kitaysky 2001). After hatching, the chick is brooded constantly for the first 5–7 days, after which it is attended briefly during provisioning bouts. Chick development is slow, with a typical nestling period of 34–46 days (Piatt and Kitaysky 2001). Both parents feed the chick, transporting several fish in the bill and dropping them in the nest chamber near the chick. Chicks on Duck Island are delivered about three to six meals a day on average (Harding 2001).

SELECTION OF NEST SITES

Toward the end of the incubation period, we searched puffin breeding habitat around the island for visible nest chambers with active nest sites. Twenty-three nest sites were found that could be easily reached. Where hatch date was unknown, chicks were aged (to within 4 days) using the following linear regression of age on wing length for chicks of known age (means \pm SE, using all known-age chicks in this colony over 5 years of study; $n = 67$ chicks, Harding 2001): chick age (days) = $0.26 \pm 0.01 \times \text{wing length (mm)} - 0.54 \pm 0.60$ ($r^2 = 0.86$).

The mean chick age at the start of the experiment was 12 days (range 9–21 days). Chicks were paired by age to control for possible differences in parental breeding performance related to hatching date (Harris 1980), and then chicks in each pair were randomly allocated to either the experimental (supplemented; $n = 11$) or control group ($n = 12$). There was no difference in mean age of the two groups of chicks ($t_{20} = 0.99$, $P = 0.33$). On 6 August, the day prior to the start of the experiment, the mean \pm SE age of control chicks was 12.0 ± 0.9 days; experimental chicks 11.0 ± 1.1 days. One experimental chick died during the study, leaving 10 chicks in the experimental group.

SUPPLEMENTAL FEEDING

Nutritional status of the experimental chicks was manipulated by supplementing their diet between 11 and 19 August. Within two hours of midday, all nest sites were visited daily and experimental chicks were fed. At control nests, we mimicked the disturbance caused by supplementary feeding, but left no food. From 11 to 19 August, each experimental chick was supplemented with 100 g day^{-1} of age 0 (born within the year prior to capture) Pacific sand lance (*Ammodytes hexapterus*) caught locally with a midwater trawl and frozen until used in the experiment. Sand lance dominated the diet of Horned Puffins on Duck Island, constituting 90% ($n = 158$) of chick diet at nests monitored separately from this study in 1998 (Harding, unpubl.). Thawed fish were placed in the nest chambers of experimental sites. Chicks ate all supplemental food each day. The visual influence of the supplemented fish load would have had no, or rare, influence on the parent's behavior since checks on experimental chicks after supplementary feeding showed all food to be eaten within 30 min, and uneaten food was never found at a nest-site. We assumed that adult puffins did not eat the supplement because captive adult Atlantic Puffins will not take fish from the ground (Wernham and Bryant 1998).

The energy contents of supplemental fish were calculated using published wet mass energy density conversions (Van Pelt et al. 1997). Fish were frozen for less than 4 weeks and we assumed no change in energy density due to freezing. The 100 g of sand lance provided an extra 506 kJ per day. The supplementary ration was more than the daily maximum usually delivered to Horned Puffin chicks (Kitaysky 1996), and therefore likely to promote a maximum reduction in parental provisioning.

CHICK NUTRITIONAL STATUS

Chick body mass and chick growth rate (mass) were used as indicators of the chick's nutritional status. Body mass was measured to the nearest 1.0 g using a spring scale. Repeat measurements, taken in accordance with the procedure as recommended by Barrett et al. (1989), were within 1.0 g.

PARENTAL PROVISIONING

Since feeding rates of both Atlantic and Horned Puffins can vary from day to day (Ashcroft 1979; AMAH, pers. obs.), provisioning was quantified during sessions of two consecutive days, defined as a 48-hr period from dusk to dusk. In the first session (prefeeding) we measured provisioning prior to supplementary feeding (7–8 August), and in the second session (postfeeding) we measured provisioning following seven days of supplemental feeding (18–19 August). Provisioning effort per chick was quantified in terms of total prey biomass (by species) delivered over the two 48-hr food-restricted periods. Fish biomass was then converted to kJ energy using published wet mass energy density conversion factors (Van Pelt et al. 1997).

The low density of nest sites on Duck Island, and the high proportion of sites in crevices or caves with multiple or shared entrances, prevented the simultaneous observation of food delivery to multiple nest sites. In order to obtain an accurate measurement of

deliveries, a black pipe-cleaner halter was used to prevent prey consumption by chicks and allow collection of individual prey items. The pipe cleaner was twisted around the base of the bill to prevent bill opening, and fitted loosely around the neck and head to anchor the halter in place. Chick movement, breathing, and vocalization were not impaired, and the halters were designed to minimize bulk and visual impact. It is possible that the halters affected provisioning or chick growth; sample sizes were insufficient to allow a third, nonhalted control group. However, any effect of the halter on parental provisioning or chick growth would be consistent across experimental treatments, and we therefore had confidence that any differences between treatments would be due to the manipulated nutritional status.

Young Horned Puffin nestlings receive about 3 (range 2–6) meal deliveries per day (Piatt and Kitaysky 2001). In order to prevent alteration of parental behavior due to the presence of uneaten fish in the nest chamber, we visited all nests 4–5 times daily at regular intervals throughout the food-restricted periods and collected all fish found in nest chambers. The first check was conducted within an hour of dawn and the last check within an hour of dusk. We assumed that all fish brought to the chick were left in the nest chamber. Fish collected were identified, weighed (using an electronic balance, to the nearest 0.01 g) and measured (length to tail fork, in mm).

In the event that young chicks were vulnerable to short-term starvation, halters were removed for 30 min on each day during the first noosing session, and chicks were fed a total of 60 g of sand lance over the 48-hr period. Horned Puffin chicks receive an average range of 7–26 g of food per day (Kitaysky 1996). On both days during the second noosing session, by which time chicks were presumed to have more resilience to food deprivation, all chicks were refed the total amount of food provisioned by their parents. In addition, the experimental group continued to be fed the extra 100 g of sand lance per day.

STATISTICAL ANALYSIS

Between-treatment differences in chick body mass, chick mass gain (g), and estimated chick age were examined with an independent-sample *t*-test. Mass and energy content of prey delivered by the parents in the two treatment groups were compared using a Mann-Whitney *U*-test because the data were not normally distributed. A general linear model was used to separate the influence of treatment and age on the kJ of prey provided. All statistical tests were performed with MINITAB (1996). Statistical significance was assumed at $P < 0.05$. Unless otherwise indicated, values reported are means \pm SE.

RESULTS

CHICK NUTRITIONAL STATUS

On 6 August, prior to the period of supplemental feeding, there was no difference between the two groups in chick body mass (Fig. 1; control mean = $208.5 \pm 15.8 \text{ g}$, experimental mean = $219 \pm 16 \text{ g}$; $t_{21} = 0.5$, $P = 0.32$). Experimental chicks gained more body mass ($8.5 \pm 0.7 \text{ g per day}$) during the supplemental

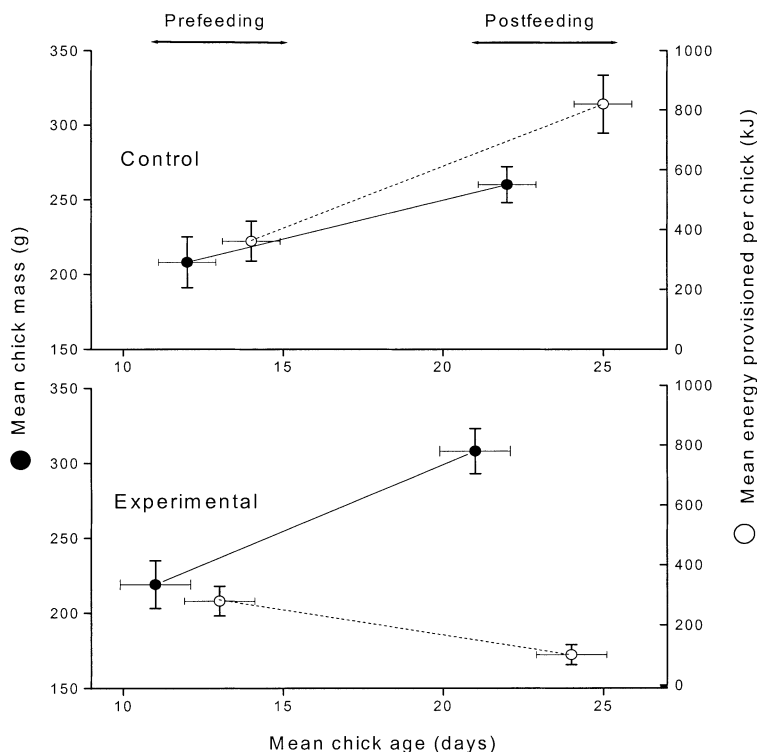


FIGURE 1. After six days of supplemental feeding, experimental Horned Puffin chicks had gained more mass than an unfed control group, and their parents subsequently brought them much less food energy than in the control group. Food energy (unfilled circles) delivered to control and experimental chicks during the 48-hr prefeeding session did not differ. Chick mass (filled circles) was measured 1–2 days prior to the prefeeding and postfeeding sessions; energy means represent total kJ provided to chicks during each 48-hr session. Error bars equal SE; $n = 12$ chicks for control group, and 11 for prefeeding and 10 for postfeeding experimental group.

feeding period than the control chicks (4.9 ± 0.9 g per day). On 16 August, after six days of supplemental feeding, experimental chicks had higher mean body mass than control chicks (Fig. 1; mean experimental chick mass = 309.3 ± 15.2 g, mean control mass = 260.1 ± 12.2 g; $t_{18} = 2.5$, $P = 0.01$).

PARENTAL PROVISIONING

We collected a total of 1049 prey items. Sand lance was the dominant prey species, constituting over 92% of the diet of both experimental and control chicks. Most other prey were salmon (*Oncorhynchus* spp.) and capelin (*Mallotus villosus*), constituting 4.5% and 2.5% of the diet respectively. Invertebrates comprised <0.5% of chick diet.

The total mass of food delivered to individual chicks during the prefeeding session did not differ ($U_{11,12} = 48$, $P = 0.28$), between the two groups (mean control mass = 67 ± 12 g, mean experimental mass = 50 ± 9 g). During the postfeeding session, however, control chicks received a greater mass of prey (155 ± 18 g) than the experimental chicks (20 ± 7 g; $U_{10,12} = 20$, $P < 0.001$).

The total energy delivered to chicks during the prefeeding session did not differ between experimental

(286 ± 49 kJ) and control (361 ± 66 kJ) groups (Fig. 1; $U_{11,12} = 52$, $P = 0.41$). During the postfeeding session, however, there was a large difference (Fig. 1; $U_{10,12} = 3$, $P < 0.001$) between the two groups in energy provided. Energy provisioning to experimental chicks (101 ± 34 kJ) was reduced by 88% compared to control chicks (820 ± 97 kJ). Three of the 10 experimental chicks received no food during the postfeeding session. Total food energy delivered differed between the two treatments ($F_{1,19} = 41.8$, $P < 0.001$), but was independent of chick age ($F_{1,19} = 0.9$, $P = 0.36$).

DISCUSSION

Adult provisioning was strongly affected by the nutritional status of chicks. After seven days of supplementary feeding resulted in a significant increase in body mass of experimental chicks, parents provisioning those chicks delivered 87% less food in terms of mass, or 88% less food in terms of energy, than parents of control chicks. The similarity between mass and energy delivered reflected the dominance of a single prey species in diets. We interpret the reduction of parental provisioning and the higher mass gain of supplemented chicks as evidence that Horned Puffins can decrease

provisioning in response to the enhanced nutritional status of their chick. However, nutritional status comprises both chick hunger and chick body condition, and it is difficult to distinguish between these effects on parental provisioning. Parents may have been responding to short-term changes in chick hunger level associated with the daily food supplements, or longer-term changes in the chick's body condition, or both. In any case, parents demonstrated an ability to decrease their level of food provisioning in response to reduced chick need.

The reduction in food delivered to experimental chicks during the postfeeding session is unlikely to be due to the tendency of adults to decrease food delivery prior to fledging (Harris 1984). Chicks in the two groups were of similar age, and the age range of experimental chicks during the postfeeding session ranged from 20–32 days, younger than the average Horned Puffin fledging age of 34–46 days (Piatt and Kitaysky 2001). The absence of food delivery to 3 of the 10 experimental chicks during the postfeeding session was not the result of abandonment since we observed parents making subsequent visits to these sites.

This study provides further evidence of the ability of parents to decrease provisioning effort in response to reduced chick need, yielding similar results to supplemental feeding experiments on the closely related Atlantic Puffin (Cook and Hamer 1997, Wernham and Bryant 1998). In order to more fully understand parental constraints and the different selective pressures involved in the regulation of provisioning, it would be useful to examine whether puffins can *increase* provisioning effort in response to increased chick needs. There is some evidence that suggests Atlantic Puffins are able to increase provisioning effort, with an increase in the number of feedings observed in response to playback of chick begging calls (Harris 1983). Atlantic Puffins also increase food delivery to older chicks in the middle third of their six-week development (Harris 1984), when the combined requirements of body maintenance and growth are highest, and control Horned Puffin parents in this study increased their provisioning to older chicks during the second food-restricted session. Furthermore, a cross-fostering experiment manipulating chick age in Atlantic Puffins found that parents were able to increase provisioning to larger and older foster chicks (Johnsen et al. 1994).

Puffins exhibit high temporal and geographical variation in chick growth and fledging age and mass, traits considered to reflect an unpredictable food supply. Under such conditions, a flexible provisioning strategy may be beneficial. In years of good food availability, parents in good body condition may increase their food provisioning without risking their own survival (Erikstad et al. 1997). Since there is a positive relationship between feeding rate and chick survival (Barrett and Rikardsen 1992), the benefits of a parent's ability to increase food deliveries are clear. However, the possible costs of energy expenditure and predation risk also need to be examined.

Conversely, in conditions of poor food availability, the reduction of food provisioning may be an impor-

tant mechanism to reduce parental effort for a long-lived species with a single-egg clutch. The physiological flexibility of puffin chick growth, fledging age, and fledging mass (Kitaysky 1996), combined with the protection afforded by the burrow and crevice nests of puffins, may allow parents to reduce food provisioning and still rear a chick to fledging with minimal effect on their own body condition and survival. The high and relatively constant reproductive success of Horned Puffins across their North Pacific range (Piatt and Kitaysky 2001), coupled with the high annual and geographic variation in chick growth and fledging age, suggests a flexible provisioning strategy that works in concert with chick growth plasticity in a species subject to a variable food supply. Variation in food availability between populations may even lead to colonial differences in the response and sensitivity to chick begging behavior.

Evidence that chicks of many species can manipulate parental food delivery is growing (e.g., Price 1998, Clark and Lee 1998, Granadeiro et al. 2000, Kitaysky et al. 2001). Experimentally comparable inter- and intraspecific studies at single colonies among years, and among different colonies, are needed to increase our understanding of mechanisms regulating food provisioning and the selective pressures involved in the regulation of reproductive effort. Better knowledge about the factors that influence and regulate provisioning effort in puffins could enhance our understanding of the behavioral ecology of provisioning in general, and could allow better specific prediction of the breeding ecology and population dynamics of seabird populations subject to changes in food availability.

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